

tilization. This reduction and doubling of the chromosomes is strongly believed to be closely connected with the hereditary transmission of characteristics from two parents, and seems to have to do with the changes in the germ plasm that produces variation within the offspring of the same pair of parents.

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#### THE GROWTH OF A COMPOUND EYE

As is well known to students of insect life, there is a period between the larval and adult stages of development when important structural changes take place. For instance, take one particular type of organ, such as the eye. In a moth larva such as the Tussock, *Notolophus leucostigma*, the larva has several single eyes grouped on each side of the head. Somewhere between the time of its entering upon the pupal stage and its emergence therefrom as an adult it exchanges these simple larval eyes for an elaborate pair of compound eyes. How it does this, and what becomes of the old larval eyes, is a process so well hidden from view in the pupal case that only cytological work can reveal the secrets.

When ready to pupate the larvae of most moths seek various sheltered positions in which they undergo their final molt or shedding of the larval cuticula. This leaves the hypodermal (epidermal) cells of the creature raw, under which conditions they exude a fluid which hardens and forms the pupal case.

As most individuals of a brood undergo their stages at similar intervals one may by collecting a number of pupae at this stage get material for studying not only the stages of the eye, but of other structures as well. By selecting individuals, at say two-day intervals from the first day of pupation onward, we will get a series showing the progressive development of the parts.

The pupa so selected should be opened in the back by a sharp instrument to allow the rapid penetration of the killing and fixative fluids. If any particular part of the tissue is wanted, it is necessary to be very careful, in making openings, not to injure or deform the tissues in the immediate vicinity.

During the pupal life, two very important and entirely opposite processes are necessarily very active. One is the breaking

down and absorption of the useless larval structures. This destructive process is carried on by two different factors:—by phagocytes, a special form of cell which gives out certain products which break down and disintegrate passive adult cells into blood pabulum; and by natural breaking down processes of cells which have lost their functional places in the changing economy. The other or opposing process is one of rapid cell division and growth of new types of cells which are to become differentiated into new adult organs.

In the first class of structures which disintegrate, we may include the larval types of eyes. These, following all the previous larval molts, have grown a new cuticula and have retained their function; but now it is no longer so. With this last molting process they immediately collapse and shrink toward the brain to which they are attached. Here they will be recognized in the photos of subsequent stages as the dark pigmented masses at the posterior lobe of the brain. Finally through growth of the brain they come to lie well down on the stalk of the lobes.

Let us now turn toward another aspect of the head of the creature. During larval life the cheeks of the larva were plump with masses of muscle which were absolutely essential in working the cutting jaws during the active voracious life of the caterpillar. From now on these muscles are useless, as the biting jaws will never be used again. These rounded cheeks are destined to become the seat of a new activity; they are to become the site of the enormous compound eyes of the adult insect, containing many hundreds or thousands of eyes, as the case may be. The phagocytes have been active for several days and there is a large cavity filled with body fluid in each cheek. This blood fluid contains numerous phagocytes, many broken down tissues, and many fat cells which enter through the wide neck opening from the thorax. In the meantime, the ectodermal layer of cells has proliferated to quite an extent so that there is a seemingly chaotic mass several cells deep.

Fig. 1 (Plate VII) represents a frontal section of the head in the region described above, passing through both brain lobes and through the regions to be occupied by the compound eyes. The

larva is in about a four-day stage of pupation. This photograph may serve as a topographic chart to which may be referred all the special organs mentioned in later figures.

Fig. 2 is an enlarged view of the optical elements of the same 4-day stage. Practically all the cells which are to form the future eye tissue are now present and there is to be no increase in number henceforth. Later change is due to growth and differentiation of these cells. That is, the cytoplasmic vegetative systems of these cells are to grow into their hereditary forms, and the individual cells are to adjust themselves into their peculiar group relations. What looks at this stage as a hopeless jumble of cells without order or form, is the foundation of an order which will develop itself with remarkable speed.

If we now turn to the next or 5-day stage, shown in Fig. 3, we shall see that the cells have undergone a remarkable arrangement into definite groups, each of which is an exact duplicate of its neighbor. Also within these groups, they are beginning to show definite shapes and relations to each other. Their vegetative systems also grow to show more of their future structural characters. Order has appeared out of seeming chaos.

By examination of the 6-day stage, Fig. 4, we will see that the mass of optical elements has doubled in thickness by the growth of the cell systems.

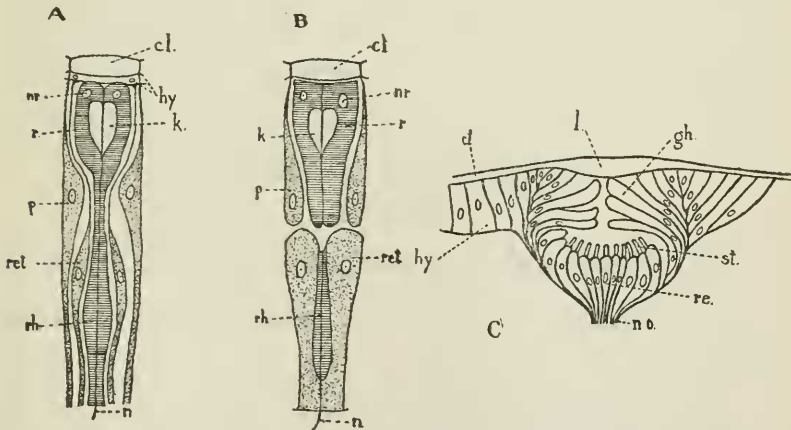
Fig. 5 is a view of the optic lobe of the brain at this same 6-day stage. There has grown a bewildering complexity of elements here. The large dark pigmented mass is the rudiment of the larval eyes.

We will now turn to the 8-day stage well shown in Fig. 6. Here we find the cells again doubled in bulk as compared with the 6-day stage. The pigment cells and nerve cells are greatly elongated and now reach backward nearly to the brain itself.

A cross section of these groups of optical elements is shown in Fig. 7 (Plate VIII). Here the elements are seen to be grouped into hexagons, an effect produced by pressure of the opposing groups of cells. Toward the margin of the section the elements are, of course, cut obliquely. A surface view of the cornea, as

Fig. 8, shows the beautiful regularity of the hexagonal visual elements.

As to the cytological structure of these compound eyes, there are several views. Two of these taken from Lang's "Comparative Anatomy," pages 470 to 471, are here illustrated in diagrams (text figures) A and B. These authors both consider the hypodermal layer of cells as distinctly a layer by itself. We can hardly agree with this view, however. In all the types of eyes examined we find that in the early stages there is but a single layer of cells in the hypodermis. Later some of the cells draw inward and by division give rise to other cells which form the ommatidium group. So it appears to us that the whole group of cells is strictly hypodermal in origin. These cells now elongate, forming spindle shaped cells which extend more or less the entire depth of the ommatidium. Such elongated undifferentiated cells are seen in the eye of the



The structure of an ommatidium (single eye) of the compound eye:—A, according to Patten's view; B, according to Grenacher's view. *cl*, cuticular corneal lens; *hy*, hypodermis cells; *r*, retinophorae-crystal cells; *nr*, nuclei of the same; *k*, crystalline cone; *p*, pigment cells; *ret*, retinulae; *rh*, rhabdome; *n*, nerve.

According to Patten (A) the ommatidium is apart from the corneal hypodermis, of one layer, all its elements passing by means of thin processes through its whole thickness from the base of the corneal lens; according to Grenacher the ommatidium, apart from the corneal lens, consists of two layers. (Taken from Lang's Comparative Anatomy, page 471.)

C, Section through the ocellus of a young *Dytiscus* larva (after Grenacher.): *ct*, chitinous cuticle; *l*, cuticular lens; *gh*, cells of the vitreous body; *hy*, hypodermis; *st*, rods; *re*, retinal cells; *no*, optic nerve.

male Ephemera, Fig. 9, (1). The nuclei of these cells gradually migrate as they grow to the localities where they are found in the adult eye.

The corneal hypodermis consists of a varying number of cells arranged in hexagons following the shape of the compressed ommatidium below. When the crystal cells begin their enlargement these corneal cells are displaced by their outward growth and finally come to lie around the base of the cone group of cells. This is well shown in Fig. 9, (2) of the Ephemera eye. They are thus seen to be the last of the hypodermal cells to assume the elongated spindle shape lying vertical with the rest of the ommatidium group. See also Fig. 10. So we consider there is really but one layer in the eye when they have all reached adult stages. In both the diagrams the rhabdome should have been shown as a nucleated cell, being the central cell of the group of reticular cells. The nucleus of the rhabdome cell finally comes to lie at the inner margin of the eye. We believe, therefore, that the usual method of diagramming of the optic nerve is wrong, the central reticular cell

## DESCRIPTION OF FIGURES

### PLATE VII

Fig. 1. Tussock Moth, 4-day pupal stage. Frontal section thru brain and compound eye.

Fig. 2. Tussock Moth, same stage. Portion of developing eye much enlarged.

Fig. 3. Same, 5-day pupal stage. Region similar to Fig. 2.

Fig. 4. Same, 6-day pupal stage. Similar region.

Fig. 5. Same, 6-day pupal stage. Optic lobe of brain.

Fig. 6. Same, 8-day pupal stage. Region similar to that of Figs. 2-4.

### PLATE VIII

Fig. 7. Tussock Moth. Eye elements cut in cross section.

Fig. 8. The corneal lenses of the compound eyes of *Tabanus astrata*.

Fig. 9. Eye of male Ephemerid: 1, spindle cells; 2, hypodermal cells; 3, rhabdome cell.

Fig. 10. Eye of a female *Rhamphomyia*—a Dipteran.

